A Study of the Hilltopping Behavior of *Pieris occidentalis* Reakirt

(Lepidoptera : Pieridae)

Jon H. Shepard

Division of Systematic Biology, Stanford University, Stanford, California[1]

The term hilltopping refers to the congregation of insects at the top of mountain peaks and other land prominences. Use of the word congregation does not imply the mass movement of insects upward in the atmosphere by air currents or other macro-environmental factors. Apparently either a local (micro-) environmental factor or the behavior of the insect is responsible for its presence at points of high relief. Hilltopping is not meant to apply to insects which are present at these points during more than one developmental stage.

Hilltopping in insects is a well established fact. Chapman (1954), Dodge and Seago (1954), and others have observed that usually a much higher percentage of one sex is present. Males generally are the common sex and are often the only sex involved. Beall (1953) and Guppy (1953) brought this phenomenon to the attention of lepidopterists. Several other notes have published records of hilltopping in a variety of butterfly species (see literature cited).

Various explanations of this type of flight in butterflies have been made. Merritt (1953) cited five reasons for the behavior: (1) food plant, (2) winds, (3) tropism, (4) surplus males, and (5) liking hilltops. Merritt found none of these satisfactory. Beall (1953) and Knudsen (1954) considered two other plausible explanations. Beall suggested the occurrence of short unidirectional flights ending at the hilltops. Knudsen contributed the idea that thermal updrafts might draw the butterflies upward.

Ants, ladybugs, horseflies, tachinid flies, and blowflies are examples of other insect groups which congregate at hilltops. All are known to be capable of flying long distances. Buprestid and elatrid beetles behave in this way also, however, little is known of their habits in other situations. Poulton (1904) suggested that the movement of insects to hilltops represented congregation at a breeding site. This may be true in some groups of insects where both males and females are found on a hilltop with breeding and feeding sites far removed, e.g. ladybugs or

---

[1] Current address: Department of Biology, Notre Dame University of Nelson, Nelson, British Columbia.

The Pan-Pacific Entomologist 42: 287–294. October 1966

ants. No evidence of this type of behavior has been seen in butterflies.

To better understand hilltopping behavior in a butterfly species, a mark and release study of *Pieris occidentalis* Reakirt was undertaken on a peak in northern Washington.

Methods and Description of the Area of Study

In two previous summers, it had been noted that several species of butterflies characteristically flew at or near the tops of mountain peaks in the Cascades of northern Washington. During the summer of 1963, the author was stationed on a U.S. Forest Service lookout in northern Washington. It was decided that a study of this flight behavior would be attempted through capture-recapture methods.

Pieris occidentalis was chosen for this study because it is the most common hilltopping species in the area. There are several other species which are also abundant at or near the tops of peaks in the northern Cascades. These are *Parnassius phoebus* Fabricius, *Papilio zelicaon* Lucas, *P. indra* Reakirt, *P. eurymedon* Lucas, *Speyeria hydaspe* (Boisduval), *S. mormonia* (Boisduval), *Boloria astarte* (Doubleday), *B. titania* (Esper), *Euphydryas anicia* (Doubleday), *E. editha* (Boisduval), *Vanessa cardui* (Linnaeus), *Oeneis melissa* (Fabricius), *Agriades glandon* (Prunner), and *Hesperia comma* (Linnaeus). Butterflies of the genera *Parnassius, Papilio, Euphydryas, Agriades,* and *Hesperia* do not fit the definition of hilltopping given above. Adults of both sexes are present and, also, the food source is near. *Boloria* and *Oeneis* also seem to be attracted to food sources, but in *O. melissa* the males greatly outnumber the females and the food plants of the *Boloria* are not yet determined. It is assumed that *Boloria* and *Oeneis* species go through all developmental stages on or near the top of mountain peaks and are not attracted at the adult stage only.

Vanessa cardui, Speyeria sp., and *Pieris occidentalis* are a heterogenous ecological grouping. *Vanessa cardui* was seen only in the late afternoons. This behavior is similar to that at lower elevations where *Vanessa* and *Nymphalis* species can be seen alighting in places where there is still late afternoon sunshine. Only the *Speyeria* and *P. occidentalis* adults are found at the tops of hills for reasons that are not directly related to their reproductive cycle. The *Speyeria* were not locally abundant on Slate Peak and thus were not available for study.

Slate Peak lookout (Okanagan County, Washington, elevation 7400 feet), where this study was carried out, is 18 miles south of the Washington-British Columbia boundary and it straddles the east-west divide of the Cascade Mountains. There are three major ridges extending

to the northwest, northeast, and southeast, respectively. The northwest ridge has no prominent points. The northeast ridge has a prominence named Haystack Mountain. The southeast ridge has a gently rising extremity. The prevailing winds are from the west-southwest. Thus air currents generally move at right angles to the main ridges. The top of Slate Peak has been leveled off to provide space for a radar installation which is no longer in operation. The flat surface is approximately 150 feet across. The only man-made structures now present are a lookout tower (42 feet high), a one-story ground house, and an out-building. The ground is covered with rock and gravel. Relatively little vegetation is present because of the disturbances caused by construction of the buildings in the last five years. Also there is only sparse vegetation for about 40 feet down from the top on all sides of the peak. Haystack Mountain is 7300 feet in elevation and generally like Slate Peak, except that there is some vegetation in the form of Compositae, grasses, and sedges on the flat top.

Pieris occidentalis was common on Slate Peak, Haystack Mountain, the connecting ridge on its eastern slope, and the ridge extending to the southeast; it was uncommon on the northwest ridge. The only two females seen during the summer were taken on the west slope of the southeastern ridge; this locality is shown on fig. 1. On the lower slopes toward Harts Pass the species was not common.

The mark-recapture technique for study of diurnal Lepidoptera populations, as refined by Ehrlich and Davidson (1960), was employed to record the presence of *P. occidentalis* on Slate Peak and any subsequent moves to other areas. Specimens were marked only on Slate Peak. Therefore, when looking for individuals in other localities, time was not consumed in marking new individuals and in recording data. All roads and trails on the map (fig. 1) were collected by several people in an attempt to recover marked individuals. Mr. John Pederson, stationed at the guard house at Harts Pass (fig. 1), collected and observed in this area. Several collectors contributed to the recaptures near Slate Peak during one or more days of the summer.

RESULTS AND OBSERVATIONS

Forty-one male specimens of *Pieris occidentalis* were marked and released in 24 days. In comparison with other years, the actual number of males seen was small. In past years, eight to ten individuals have been seen flying together; often, one was pursued by the others and the group flew in a linear formation. In 1963, no more than five or six males were seen on Slate Peak at one time. This decrease in numbers

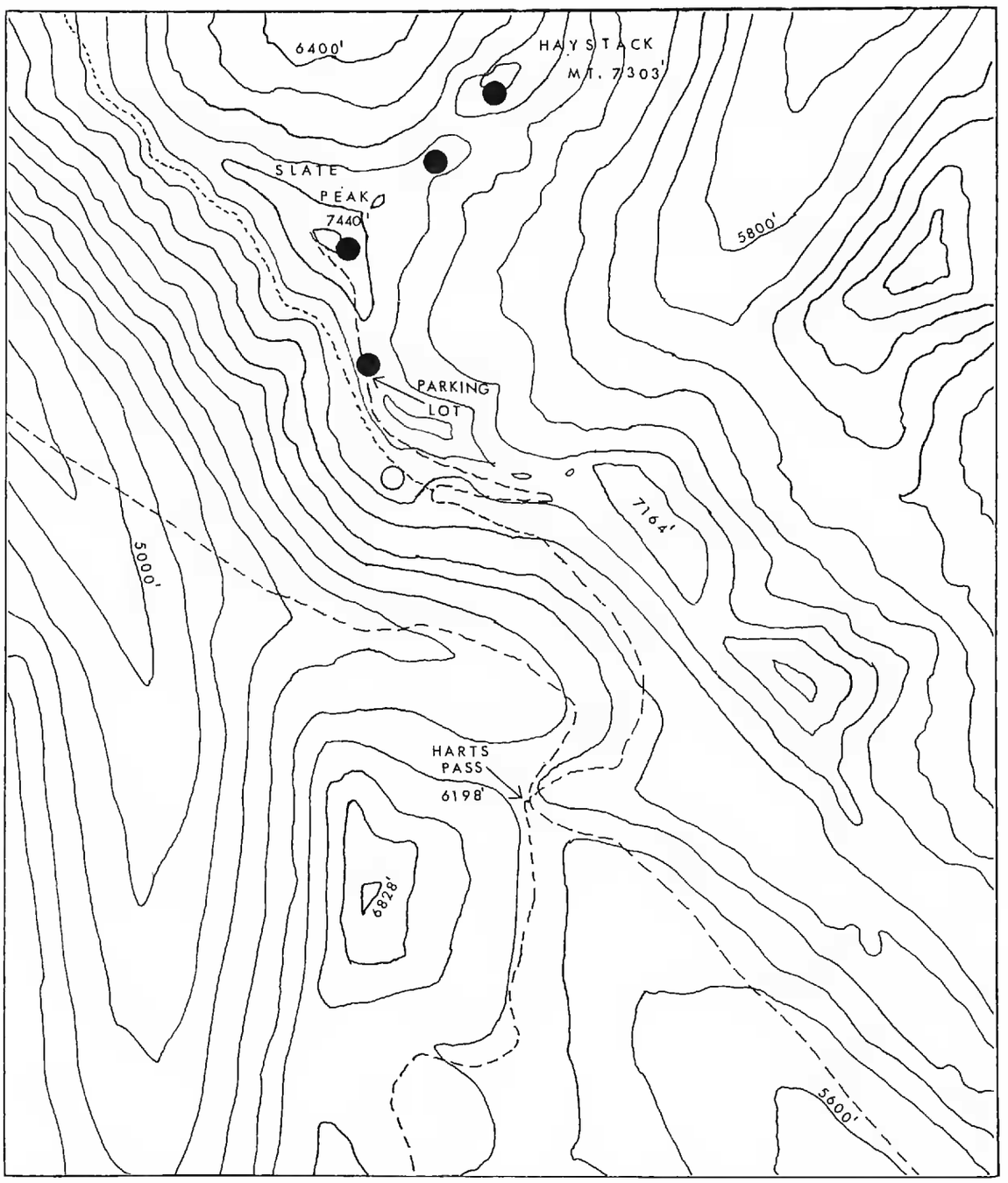

Fig. 1. Map of Slate Peak and area. Solid circles indicate areas where males were recaptured. Open circles indicate areas where females were taken. U.S.G.S. Map, 1 : 24,000, Slate Peak, Washington.

is possibly caused by the fluctuating weather conditions in the summer of 1963: brief periods of warm, favorable weather were interrupted by cold, rainy days (Table 1). The entire population could not have emerged at one time and mortality rate was higher because of the bad weather.

Seven specimens were recaptured at least once. This represents 17% of the population. This figure is low compared with Ehrlich's (1961)

Table 1. Data on capture-recapture of *Pieris occidentalis* Reakirt.

Time	10:00	11:00	12:00	1:00	2:00	3:00
July 13	1, 2, 3, 4	5, 6, 7, 8, (1)		(1), (8)	9	
...						
18	10, 11	12, 13, 14, 15, 16, 17, 18				
19	19, 20, 21, 22, 23					
...						
26					(6)	
27	(1), (6), 24, 25	26, 27, 28, 29			30, 31, 32	
28	(32), 33, 34	35, 36, 37, 38, 39, 40	(6)			
...						
Aug. 2					(26), (28)	
3						(30)
4			41			

() = recapture; (26), (28), (30), (32) = specimens recaptured some place other than Slate Peak.

work on *Euphydryas editha* (Bdv.) (Nymphalidae) which recorded 51% recaptures. It is also low compared to the 60% recaptures in a population of *Parnassius phoebus* (Papilionidae) (J. Shepard and N. West, unpublished). Nevertheless, the 17% for *P. occidentalis* compares favorably with results for other Pieridae; for example, 10% for *Eucholoe ausonides* Lucas (J. Shepard and N. West, unpublished). Other North American species have intermediate percentage recaptures. Ehrlich, Emmel, and Soulé (unpublished) recaptured 25% of *Erebia epipsodea* Butler (Nymphalidae). Thirty-three percent of *Plebejus icariodes* (Bdv.) (Lycaenidae) were recaptured in a study conducted by T. C. Emmel (unpublished).

Of the seven specimens recaptured, three were recaptured on Slate Peak (Nos. 1, 6, 9); one was taken on Haystack Mountain (No. 26), one half mile northeast of Slate Peak; two specimens were taken one quarter mile northeast of Slate Peak (Nos. 28, 32); and one was taken one quarter mile south of Slate Peak (No. 30). These recaptures are shown in fig. 1. Although several specimens were netted on the northwest ridge of Slate Peak, no marked specimens were captured.

As shown in Table 1, most initial captures, releases, and recaptures on Slate Peak were performed between 10:00 a.m. and 12:00 a.m. This was not an artifact of sampling. On all days when weather permitted, hourly examination was made of the area where specimens were marked and released. Specimens were captured, marked, and released in less than thirty minutes. Most specimens which show hilltopping behavior would do so early in the morning, returning to the lower slopes between

1:00 p.m. and 2:00 p.m. The hourly recurrence of the day's specimens was not recorded after the first day of the study. It was felt that frequent netting of butterflies, placing them in glassine envelopes, and later releasing would interfere with "normal" flight activity. A specimen was retaken in one day only if it could not be ascertained whether it had been marked or recaptured that day. Most specimens would settle on a rock long enough for the wing marks to be read and their identity determined.

Discussion

From the above described situation and data obtained from the mark-recapture of *Pieris occidentalis* several questions concerning the phenomenon of hilltopping can be partially answered. Also, the need for further research is clearly indicated.

The definition of hilltopping behavior given in the introduction of the present paper eliminates food plant presence as a cause of hilltopping (Merritt, 1953). Any species of insect whose food plant is present is interpreted as responding to a hilltop in a manner similar to its response to any food source. If a species is congregated on hilltops because the food source is in excess there, this is a response to the food and not the hill.

Terms such as "tropism" or "liking hilltops" (Merritt, 1953) do not give causative explanation for hilltopping. They only categorize the type of behavior.

Wind as a factor (Merritt, 1953) in hilltopping is not a causative agent. In actuality the numbers of *P. occidentalis* hilltopping on a given day is in inverse ratio to the strength of the wind. Even the weakest flying butterflies such as *Erebia epipsodea* Butler, *E. vidleri* Elwes, and *Boloria epithore* (Edw.) either fly against mild winds or stop flying in heavy winds. Therefore, these butterflies are not forced to the top. On Slate Peak *P. occidentalis* had to actually fly against the wind to arrive at the very top. On the west edge of the peak where the winds were blowing directly up out of the valleys, no specimens were ever seen reaching the top. All specimens arrived at the top from the east slopes, where wind movement was limited until the top of the peak was reached.

The idea that a surplus of males in a population causes many of them to congregate on hilltops (Merritt, 1953) or in other areas, i.e. mud puddles, may be a complete misconception on the part of observers. In at least one butterfly species, *Euphydryas editha*, the extrovertive flight behavior of male insects in a population makes it appear that

more males than females are present in the field (Ehrlich, 1965). Studies of sex ratio in the field for pupae of *E. editha* show even a slight predominance of females (Shepard, unpublished).

Only the causes of hilltopping that Beall (1953) and Knudsen (1954) have proposed seem meaningful in view of the data obtained during the mark-release study. Beall suggests that hilltopping butterflies participate in short, unidirectional flights that often end up on the top of hills. Butterflies and other insects presumably congregate there because the hilltop interrupts the unidirectional flight. *Pieris occidentalis* could be corresponding to this type of behavior. The low 17% recaptures for *P. occidentalis* suggest that individuals of this species have a home range larger than that in most butterfly species, or that they have no home range at all, and therefore a longer unidirectional flight. In other species, such as *Euphydryas editha* (Ehrlich, 1961), *Parnassius phoebus* (Shepard and West, unpublished), and *Plebejus icariodes* (Emmel, unpublished) the higher percentage of recaptures is correlated with close association to food plant, and with "intrinsic barriers" (Ehrlich, 1961) to movement. *Pieris occidentalis* and other Pieridae (*Eucholoe ausonides*) appear not to have intrinsic barriers to flight. If present, these barriers are much less intense and are easily overcome.

Beall's suggestion needs further study before it is to be considered the cause of hilltopping. First, it should be established that there are unidirectional flights of ¼ to ½ mile where *P. occidentalis* is found in a relatively flat area. Second, Knudsen's (1954) suggestion that thermal updrafts are the cause of hilltopping behavior must be thoroughly investigated. From this study it would appear that thermal updrafts are important. Most specimens arrived at the top in early morning from east slopes where thermal updrafts would start first and be the strongest.

Summary

Previous explanations of hilltopping behavior in butterflies have been based on casual observations. They were insufficient and often anthropomorphic. Even a definite idea of what a hilltopping butterfly is was not presented. A hilltopping butterfly or insect is defined as an insect species which is found on a hilltop in only one stage of development; the food source of the larvae is not present; the insects are not forced there by a macro-environmental factor such as strong winds. The results of a mark-release study of *Pieris occidentalis* show the following: (1) only males were observed, (2) most individuals arrived at the top of Slate Peak before noon, and (3) specimens were recaptured

on Slate Peak and other hilltops. *Pieris occidentalis*, like other Pieridae, has a large flight range. This lack of intrinsic barriers to flight combined with a positive reaction to early morning thermal updrafts is seen as the best explanation of hilltopping in butterflies. Further study, specifically of the nature of thermal updrafts in an area where there are hilltopping insects, is needed for a better understanding of this behavior.

LITERATURE CITED

ABBOTT, WALTER. 1959. Local autecology and behavior in *Pieris protodice* Bdv. & Lec. with some comparisons to *Colias eurytheme* Bdv. (Lep. Pieridae). Wasmann Jour. of Biology, 17(2): 279–298.

ARNHOLD, F. R. 1953. Notes on collecting *Anthocharis midea* and *Euchloe olympia*. Lep. News, 6(6–8): 99–100.

BEALL, GEOFFREY. 1953. Congregations of butterflies at hilltops. Lep. News, 7(2): 41–43.

CHANG, V. C. S. 1963. Quantitative analysis of certain wing and genitalia characters of *Pieris* in western North America. Jour. of Research on the Lepidoptera, 2(2): 97–125.

CHAPMAN, J. A. 1954. Studies on summit frequenting insects in western Montana. Ecology, 35: 41–49.

DODGE, H. R., AND J. M. SEAGO. 1954. Sarcophagidae and other Diptera taken by trap and net on Georgia mountain summits in 1952. Ecology, 35: 50–59.

EHRLICH, P. R. 1961. Intrinsic barriers to dispersal in Checkerspot butterfly. Science, 134(3472): 108–109.

1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge Colony. Evolution, 19(3): 327–336.

EHRLICH, P. R., AND S. E. DAVIDSON. 1960. Techniques for capture-recapture studies of Lepidoptera populations. Lep. News, 14(4): 227–229.

EMMEL, THOMAS C., AND JOHN F. EMMEL. 1962. Ecological studies of Rhopalocera at Donner Pass, California. I. Jour. Lep. Soc., 16(1): 23–44.

GUPPY, RICHARD. 1953. *Papilio zelicaon* and hilltops. Lep. News, 7(2): 43–44.

KNUDSEN, J. P. 1954. Butterflies and hilltops. Lep. News, 8(5): 141–142.

MERRITT, J. R. 1953. Butterflies and hilltops. Lep. News, 6(6–8): 101–102.

MUSPRAT, V. M. 1954. Butterflies and hilltops. Lep. News, 8(5): 143–144.

POULTON, E. B. 1904. A possible explanation of insect swarms on mountain tops. Trans. Entomol. Soc. London, 52: xxiii–xxvi.

RAWSON, G. W. 1951. Hilltops and *Anthocharis*. Lep. News, 5(6–7): 70.

1955. More on butterflies and hilltops. Lep. News, 9(4–5): 133–134.

SHOUMATOFF, NICHOLAS. 1953. The excelsior complex. Lep. News, 7(2): 38–40.

SOMEREN, V. G. L. VAN. 1955. Butterflies and hilltops in East Africa. Lep. News, 9(4–5): 127–132.